Report for 2004AZ57B: Estimation of acute upper lethal water temperature tolerances of native Arizona fishes

- Articles in Refereed Scientific Journals:
 - Carveth, C., A. Widmer, and S.A. Bonar, "A comparison of the upper thermal tolerance of native and nonnative fish species in Arizona. Transactions of the American Fisheries Society," in review.
- Dissertations:
 - Carveth, C. 2004. A comparison of the upper thermal tolerance of native and nonnative fish species in Arizona. M.S. Dissertation, School of Natural Resources, University of Arizona, Tucson, Arizona, 75 pp.

Report Follows

A. Problem and Research Objectives

Streams in the southwestern United States often experience unpredictable fluctuations in their physical conditions (Meffe and Minckley 1987). Deterioration in the quality of streams over the past 100 years has resulted in the decline or complete loss of many unique and ecologically sensitive endemic fish species. Interactions with exotic organisms, introduction of novel diseases, permanent changes in stream velocity and volume, deterioration of water quality, and alteration of habitat have all contributed to declines in abundance and distribution (Lowe et al. 1967; Moyle et al. 1986; Rinne et al. 1986; Douglas et al. 1994). Rising water temperatures have become a common concern, compelling fisheries mangers to evaluate the effects of rising stream temperatures on fish health and survival (Barber et al. 1970; Poole and Berman 2001; Chatterjee et al. 2004). In Arizona, where groundwater and snow melt have been the main drivers of stream temperature, extreme reductions in stream volume combined with loss of riparian vegetation have resulted in the loss of a buffer for temperature fluctuations. Consequently, stream temperatures are more likely to be influenced by the atmospheric temperature trends. Stream temperatures have been rising in Arizona since the early 1900s (Miller 1961), and across North America, incidences of heat death in fishes are becoming more common (Bailey 1955; Zimmerman and Kucera 1977; Matthews et al. 1982; Mundahl 1990). Mortalities related to high water temperatures occur frequently in Arizona, particularly in stagnant shallow waters with high ambient temperatures and direct sun exposure. Stream temperatures ranging from 35-40.3°C are recorded frequently in small Arizona streams during July and August (Deacon and Minckley 1974), and a few native fish species are thought to be living at temperatures close to their upper thermal limits (Lowe and Heath 1969).

Alteration of natural water temperature regimes can create a wide variety of life history, behavioral, and physiological responses in aquatic organisms (Brett 1956; Myrick and Cech 2000; Lass and Spaak 2003), and small changes in water temperature can have considerable consequences for freshwater fish (Morgan et al. 2001). Thermal tolerance in an organism is determined by a wide variety of biotic and abiotic factors, with acclimation temperature and thermal history being among the most important (Chung 2001). A temperature increase beyond the optimal range for any species can influence the capacity to function properly. Elevated temperature can diminish swimming ability in fishes (MacNutt et al 2004) and result in poor body condition by reducing cardiac performance and limiting the amount of available oxygen (Brett 1956; Fry 1967). Temperature can influence metabolic activities and have lasting effects on behavior such as predator avoidance, migration, and spawning.

Although native fishes in Arizona are considered tolerant to high temperature because their evolutionary history is rooted in a desert environment, little is known about the effects of temperature on native fishes in the Southwest. Available information is limited to field observations and a small number of laboratory studies (John 1964; Lowe and Heath 1969; Minckley and Barber 1971; Deacon and Minckley 1974). Few attempts have been made to quantify the upper lethal tolerance of multiple fish species in a single study (Deacon 1987; Smale and Rabeni 1995). Differences in acclimation temperatures,

heating rates, undefined behavioral endpoints, and other factors make comparisons among thermal tolerance values derived by a variety of methods ambiguous and difficult to interpret (Lutterschmidt and Hutchison 1997b). Lethal limits typically are comparable only when repeated when tests are run under similar conditions and similar acclimation temperatures are used (Brett 1956).

The objective of this research was to compare the upper thermal tolerance of 11 native and 7 nonnative freshwater fishes found throughout Arizona. Tests were conducted using the critical thermal method.

B. Methodology

Fish Collection

We collected eleven native and eight nonnative fish species (Table 1). Thermal tolerance data existed for the majority of nonnative fishes in our study. However, we retested these species, as it was important to use the same method to compare all species and to ensure that thermal tolerance of a species does not vary geographically. For this reason, we repeated tests for a variety of nonnative species to guarantee we had thermal tolerance data for the populations in this region.

We used small seine nets (1.6 mm) to collect wild fish in spring and summer 2003 and 2004 from Aravaipa Creek, Bonita Creek, the San Pedro River, the Verde River and Buenos Aires National Wildlife Refuge stock tanks. We collected fish of similar total length (30-70 mm) however; fathead minnow *Pimephales promelas*, yellow bullhead Ameiurus natalis, bluegill sunfish Lepomis macrochirus and green sunfish Lepomis cyanellus measured 80-116 mm TL. Gila topminnow Poeciliopsis occidentalis and Gila chub Gila intermedia were artificially propagated at the University of Arizona. Razorback suckers Xyrauchen texanus and bonytail chub Gila elegans were obtained from the Willow Beach National Fish Hatchery, Arizona. Spikedace *Meda fulgida* were obtained the Gila River (fish were propagated at the University of New Mexico) and Aravaipa Creek, to test for differences among stocks. We used guidelines provided by Arizona Game and Fish (In review) to transport fish to the laboratory. All species were treated for *Ichthyophthirius* with formaldehyde for at least 10 d upon arrival to the laboratory. Yellow grub Clinosotnum complanatum was present in approximately 20% of the Aravaipa Creek spikedace and in the majority of the loach minnow collected at the west end of Aravaipa Creek. We tested the temperature tolerance of these fishes separately to evaluate the effects of yellow grub on thermal tolerance.

When possible, we limited tests to summer so that photoperiod and other variables would be similar among tests. Long photoperiods are typically associated with increased heat tolerance (Fry 1967; Lutterschmidt and Hutchison 1997b). We tested spikedace, loach minnow and desert sucker several times throughout the year to evaluate differences in heat tolerance throughout the year.

Acclimation and Critical Thermal Method

The critical thermal method (CTM), as described by Becker and Genoway (1979) is the most common method used to quantify fish tolerance to extreme high and low temperature. CTM provides a standard for evaluating the thermal requirements of an organism and is often used to make comparison among species (Lutterschmidt and Hutchison 1997b). CTM is a preferred method in the field of thermal ecology due to the small number of animals needed and short period required to complete a test. The use of similar acclimation temperatures and heating rates also facilitates comparisons of data from several studies.

We used 200W Ebo-jager aquarium heaters to maintain ten to twelve fish of each species in well-aerated 75 L glass aquaria at 25°C and 30°C (± 0.1°C) for a minimum of 14 d. Due to limited availability, fathead minnow, largemouth bass and yellow bullhead, were tested only at 25°C. Large windows in the laboratory provided natural light cycles. Fish were fed daily to satiation a combination of brine shrimp, daphnia, bloodworms, spirulina and tropical fish food flakes. Diet composition varied by species as it does in nature. Unconsumed food was removed every other day by siphon. Approximately 20% of the tank water was removed 3-4 times each week and replaced with dechlorinated (Stresscoat®) tap water to prevent the accumulation of ammonia, nitrates and nitrites. Small water changes ensured that water temperature fluctuations were less than 1.0°C. Fish were not fed 24 h prior to testing.

We tested four fish of each species per trial. Each fish was randomly selected from the holding tank and placed in a 1-L beaker filled with water from the acclimation tank. Four beakers were placed in a 42 cm x 28 cm x 11 cm metal basin filled with water. Beakers were elevated on a metal grate, which allowed water flow to reach all sides of the beakers. A powerhead (Rio 1100) was placed in the basin to mix the water. Temperature within the basin was maintained at the acclimation temperature for 30 min prior to testing to avoid confusing handling stress with thermal stress. We used portable aerators and air stones to keep test water continually mixed and aerated. Once a testing period commenced, the basin was placed on a Fisher Scientific, 120-V, 5.4-A hotplate and temperature was increased at a constant rate of 0.3°C min⁻¹, a rate of change recommended for small-bodied fish (Beitinger et al. 2000). We adjusted settings on the hotplate at predetermined intervals to ensure a linear rate of change. Rate of change can vary within a given test $(0.3 + 0.2^{\circ}\text{C min}^{-1})$. We tested each species using a minimum of three trials to increase the amount of variation for upper lethal tolerance values of each species, to avoid any variation due to slight differences in rates of change. The rate of change is critical. An ideal rate will allow body temperature to follow water temperature without a significant time lag and avoid overshooting the upper lethal (Becker and Genoway 1979). During each experiment, one person observed the fish while a second person recorded data and maintained correct hotplate settings.

We recorded sub-lethal and lethal endpoints. Sub-lethal endpoints are referred to as CTMax endpoints and defined as the point where an animal loses the ability to escape from conditions that will ultimately lead to its death (Cowles and Bogert 1944). We

recorded several commonly cited endpoints including initial loss of equilibrium, no response to prodding, and flaring opercules. Loss of equilibrium, defined as the temperature where a failure of righting occurs, has been the most commonly reported endpoint in CTM trials (Becker and Genoway 1979). We reported initial loss of equilibrium as the CTMax value. However, because of the subjective nature of non-lethal endpoints when comparing multiple species, we also reported upper thermal limit at death. Death was defined as the cessation of opercular movements and was reported as the upper lethal limit. All fish were weighed, measured, examined for parasites, and preserved.

Data Analysis

CTMax and upper lethal temperature values were reported with 95% confidence limits. Multiple regression was used to evaluate the relationship among acclimation temperature, time of year (trial), size (TL), CTMax, and upper lethal temperature. Trial was included in the model, because for some species, individuals were caught and tested at different times throughout the year. Therefore, we tested for effects of time of year on thermal tolerance. Within species, two-sample t-tests were used to assess differences between CTMax and upper lethal temperature at different acclimation temperatures. Analysis was conducted using JMP Version 4.0.4.

Acclimation response ratio (ARR) was calculated for both CTMax and upper lethal tolerance values (Claussen 1977). The acclimated response ratio estimates the ability of fish to alter CTMax values (or other endpoints) with changing acclimation temperature. We estimated ARR values by calculating the difference between endpoint temperatures at each acclimation temperature (i.e. Δ CTM) and then dividing by the differences in the acclimation temperatures (Δ T = 5°C).

C. Principal Findings and Significance

Precision of CTMax Endpoints and Death

The critical thermal method provided a precise method for assessing thermal tolerance of the 18 species tested. The most precise endpoint was flaring opercules (SE = 0.36°C) followed by the upper lethal temperature (SE = 0.41°C) and loss of equilibrium (SE = 0.54°C). Loss of equilibrium, a widely cited endpoint, was not easily observed in some species, and signs of disorientation varied greatly by species.

Effects of Time of Year and Total Length

Total length of fish and time of year did not significantly impact CTMax and upper thermal tolerance values for any species (F- tests P < 0.05), except spikedace. Time of year was significant for upper thermal tolerance of spikedace (P = 0.007), when we included acclimation temperature and length in our model. Testing was conducted from February through October. No individuals were removed from analyses due to large size or time of year tested.

CTMax and Upper Lethal Tolerance

Upper thermal tolerance values ranged from $41.8 \ (\pm 0.2^{\circ}\text{C})$ for desert pupfish to $36.0 \ (\pm 0.4^{\circ}\text{C})$ for speckled dace when acclimated at 25°C (Table 3). Comparison of CTMax and upper lethal tolerance values indicated a strong difference among species (ANOVA *F*-ratio = 133.3, P < 0.0001) for both acclimation temperatures. Upper lethal tolerance did not seem to be grouped by taxa. Cyprinids comprised the largest family tested and had the widest tolerance, ranging from the lowest (19^{th}) to the 4^{th} highest tolerance of the eighteen species tested. The most abundant nonnative species found throughout Arizona comprised 5 of the top 8 positions with respect to thermal tolerance, all surviving temperatures close to or above 40°C .

Within species, increasing acclimation temperature increased both the CTMax (two-sided P < 0.0001) and upper lethal tolerance (two-sided, P < 0.0001). Average mean CTMax and upper lethal tolerance were higher when acclimation temperature was increased from 25°C and 30°C (1.9 ± 0.4 °C and 1.5 ± 0.5 °C, respectively).

Acclimation Response Ratio

The ability of fish to thermally acclimate varied greatly among species. Increases in thermal tolerance were most extreme within the cyprinid family, varying from 0.3°C (loach minnow) to 2.2°C (longfin dace) (Table 4).

Significance of Results

The CTM provided a precise measurement of upper thermal tolerance for all species tested. The CTM is not a test meant to mimic natural conditions, but to demonstrate relative differences in the ability to withstand high temperature among species. Under natural conditions, stream temperatures rise at a slower rate than the rate used in this study, sometimes taking 12 h to increase 5-10°C. Fish typically are exposed to heterogeneous thermal environments and latency in body temperature change, when exposed to high temperatures, affords the organism time to escape potentially lethal conditions (Beitinger et al. 1977). The CTM utilizes a rapid increase in temperature (i.e. 0.3°C/min), eliminating the opportunity for acclimation to changing temperature. For this reason CTM tests typically overshoot the actual upper lethal temperature by 3-4°C (Selong et al. 2001; Carveth 2004; Widmer 2004). Consequently, our results would not accurately reflect temperatures that these species can withstand in the wild unless temperatures in the wild increase at a similar rate to the one used in this study.

According to Beitinger et al. (2000), loss of equilibrium is an ecologically significant endpoint because this is where a fish losses the ability to escape conditions that will ultimately lead to death. Loss of equilibrium is the most widely cited CTM endpoint (Mundahl 1990; Smale and Rabeni 1995; Benfrey et al. 1997; Currie et al. 1998; Diaz and Buckle 1999; Selong et al. 2001), and, as most fish recover once placed into cooler water, is the most logical endpoint when testing endangered and threatened species.

However, loss of equilibrium was the least statistically precise endpoint of the four endpoints we used. All fish experienced loss of equilibrium, but signs were more subtle in some species, specifically loach minnow and yellow bullhead, which remained on the bottom of the beaker for the majority of the test period. Several species demonstrated obvious disorientation only when prodded with a glass rod. In a similar study conducted by Lutterschmidt and Hutchison (1997a), loss of equilibrium had significantly more variance than another endpoint, the onset of spasms. The species we used did not consistently experience the onset of spasms and this endpoint was not recorded. Reaction to prodding and death were more precise endpoints than loss of equilibrium. However, flaring opercules was the most precise endpoint and most consistent among all species. We recommend that flaring opercules be used as an endpoint where precision is important especially when making comparisons among multiple species.

Body size can influence the upper thermal tolerance of fishes due to either ontogenetic differences in physiology or due to the area: volume ratio. Body temperature in poikilotherms is influences by external changes in temperature and therefore larger organisms may experience a slower rate of heat penetration, affecting upper CTM values (Becker and Genoway 1979). In a study conducted by Smale and Rabeni (1995), several fish species, including a variety of cyprinids, centrarchids, catastomids, ictalurids and poeciliids showed no indication of size-dependent variation in upper lethal tolerance. Barrionuevo and Fernandes (1995) did not find a significant effect of body size when testing the CTMax of curimbata *Prochiludos scofra*, but body size did affect the CTMin. Cox (1974) found a difference in the upper thermal tolerance of bluegill sunfish when temperatures were increased at a rapid rate, but not when temperatures were increased at a slower rate. It is unlikely that temperatures increase at such a fast pace in nature, making it unlikely that size impacts the thermal tolerance of a species in the wild. Although, we attempted to limit the size of the individuals tested, for certain species including fathead minnow, largemouth bass, yellow bullhead, green sunfish and bluegill sunfish larger fish (80-116 mm) were used. Because there was little variation in the size of these individuals, related to the other species tested, it is unknown whether the size of individuals of these species influenced results.

Desert pupfish were the most tolerant species to high temperature, with a CTMax of 41.3 \pm 0.32°C when acclimated to 30°C. Tolerance to extremely high temperature is common among cyprinodons, and these fishes are typically found inhabiting water with high temperatures. Desert pupfish can live at 38.9°C and exhibit discomfort and death at 40.6°C (Deacon and Minckley 1974). Using the same acclimation temperature as in our study, Lowe and Heath (1969) determine the CTMax for desert pupfish to be 42°C (SD = 0.3°C). Speckled dace had the lowest tolerance, with a CTMax of 35.8 \pm 0.57°C. John (1964) reported maximum thermal tolerance of 33°C for speckled dace in the wild, when fluctuations of 10-15°C were present.

In our study, the thermal tolerance of some cyprinid species approached the tolerance of the desert pupfish. Although Brett (1956) concluded that ictalurids have the highest tolerance and cyprinids have intermediate tolerance, we found that thermal tolerance was not grouped by taxa. Thermal tolerance of the cyprinids tested ranged from 35.8°C for

speckled dace to 40.5°C for longfin dace when acclimated at 30°C. Although previously studied, we re-tested several nonnative species to ensure that CTMax values were estimated for fish from this geographic area. Our results were consistent with other studies. Red shiner ranked within the top five of the eighteen species tested in this study and is known to successfully cope with extreme pH, salinity and temperature (Matthews and Hill 1977). King et al. (1985) report that red shiners experience loss of equilibrium at 36.5-38.0°C (SD = 0.41-94) when acclimated at 25°C. Similarly, loss of equilibrium was reported at 39.6° C (SD = 0.23) when red shiners from a Texas population were acclimated at 30°C (Rutledge and Beitinger 1989) (Table 2). The red shiner has become a notorious invader throughout streams in Arizona, and has been cited in the decline of several native species (U.S. Fish and Wildlife Service 1991a; 1991b). Red shiner is able to persist in environments that have been rendered inhospitable for many native fishes (Douglas et al. 1994), and can tolerate thermal shock at high and low temperatures (Matthews and Hill 1977). Data for other nonnative species was consistent with our findings. Currie et al. (1998) reported CTMax values as 36.7 ± 0.59 °C (SD) and $38.5 \pm$ 0.34°C, for largemouth bass from Oklahoma acclimated at 25 and 30°C, respectively, at a rate of change of 0.3°C/min. Similar consistencies exist for mosquito fish data presented by Otto (1973), from a population taken from Arizona State University (Table 2). Among the nonnative species tested, geographical variability does not exist when compared to the literature. Similarities in CTMax values indicate that thermal tolerance is consistent for species from different regions. This provides us with some confidence that results from different studies can be compared when similar rates of change are used.

Temperature tolerance acclimation is the process of re-establishing internal homeostasis allowing for survival in heterogeneous thermal environments. Stauffer et al. (1984) demonstrated that cyprinids possess a greater ability to acclimate to changing temperature than do salmonids. Among the eighteen species we studied, there was a large amount of variability in the ability to extend the CTMax and upper lethal limits by acclimation to higher temperatures as shown by the variation in ARR values. A limited ability for temperature tolerance acclimation indicates that the realized tolerance of a species is similar to the fundamental tolerance regardless of the acclimation temperature (Beitinger and Bennett 2000). Red shiner and woundfin *Plagopterus argentissimus* can greatly shift their CTMax in response to acclimation temperature (Deacon et al. 1987). This provides these species with an advantage in warmer, shallower and thermally variable environments. Loach minnow, Gila chub, desert pupfish and speckled dace have a limited ability to extend upper thermal tolerance, compared to Gila topminnow, bluegill sunfish and green sunfish. These data suggest that species with low ARR would be most sensitive to increasing thermal regimes, as these species have little ability to extend their thermal range. If temperatures were increased at a much slower rate than 0.3°C/min, species with high ARR values would likely have the ability to extend their upper thermal tolerance and remain active during periods of rapid temperature increase, permitting escape from stressful situations. Under natural conditions, species with low ARR values may not be able to withstand large daily and annual fluctuations in temperature. For example, loach minnow have been described as widely adaptable to varying physical conditions, including flow and substrate (Rinne 1989). As loach minnow have a limited ability to adapt to high temperature, relative to other species, temperature may be a factor limiting

their range. This may also be true for desert pupfish, which has evolved in a stable thermal environment. Desert pupfish from Quitobaquito Springs, Arizona commonly and preferentially occupy waters with temperatures from 40-41°C when water with temperatures of 30°C is immediately available to the fish (Lowe and Heath 1969). These high temperatures are only 1-2 °C below their thermal limit indicating that behavioral thermoregulation is occurring (Hutchison and Manness 1979).

Overall our results indicate that native cyprinids were less tolerant to high temperature than nonnative cyprinids and centrarchids. Evolutionary history was cited as the reason for the success of the Arroyo chub Gila orcutti in displacing the native Mojave tui chub Gila bicolor mohavensis (Castleberry and Cech 1986). Due to their evolution in fluctuating environmental conditions, including temperature, Arroyo chub are better adapted for dealing with fluctuating environmental conditions in the Mojave River. Changing thermal regimes throughout Arizona may be negatively impacting native species by exposing native fish to temperature fluctuations outside of their tolerance range and favoring some of the more heat tolerant nonnative species, which evolved with larger temperature extremes. Historically, desert streams and rivers experienced small daily and annual temperature fluctuations. Anthropogenic alteration of stream channels and riparian areas have increased the amount of exposed surface area and increased the amount of solar radiation reaching the stream, resulting in substantially elevated water temperatures (Dickerson and Vinyard 1999). Today stream temperatures throughout Arizona regularly reach 34-35°C in summer and have been as high as 40.3°C during July and August (Deacon and Minckley 1974). Although surface temperatures may have achieved such high temperatures in the past, water depth provided a buffer with water temperatures at greater depths being much cooler (John 1964; Deacon and Minckley 1974).

Temperature is only one of many abiotic factors that impacts the distribution and survival of native fishes. However, changing thermal environments in Arizona streams and rivers, such as elevated daily and annual mean temperatures, may be adversely impacting native desert fishes. Our results provide baseline data concerning the thermal tolerance of these species. More research is needed to determine the thermal requirements of native and nonnative fish species, specifically to determine interactions occurring among these species at high temperatures.

Acknowledgements

Funding for this study was provided by Water Resources Research Center, University of Arizona, Federal Grant Number 01-HQ-GR-0113; U.S. Bureau of Land Management, Arizona Game and Fish Department; the University of Arizona and T & E, Inc. We would like to thank Mike Childs, Arizona Game and Fish Department, Chester Figiel, U.S. Fish and Wildlife Service, Steve Platania, University of New Mexico, Andrew Schultz, University of Arizona, and Phil Rosen, University of Arizona, for providing some of the fish used in this study. Thanks also to Rob Bettaso, Arizona Game and Fish Department, for providing valuable information on the transport and handling of native fishes. Thanks to Peter Reinthal, William Matter and Kevin Fitzsimmons for providing

advice on the contents of this manuscript. Finally, thanks to Didio Martinez and Andrea Francis, technicians at the University of Arizona, for their dedication to this project.

Literature Cited

- Bailey, R. M. 1955. Differential mortality from high temperature in a mixed population of fishes in southwestern Michigan. Ecology 36:526-528.
- Barber, W. E., D. C. Williams and W. L. Minckley. 1970. Biology of the Gila Spikedace, *Meda fulgida*, in Arizona. Copeia 1:9-18.
- Becker, C. D., and R. G. Genoway. 1979. Evaluation of the critical thermal maximum for determining the thermal tolerance of freshwater fish. Environmental Biology of Fishes 4:245-256.
- Beitinger, T. L., W. A. Bennett, and R. W. McCauley. 2000. Temperature tolerances of North American freshwater fishes exposed to dynamic changes in temperature. Environmental Biology of Fishes 58:237-275.
- Beitinger, T. L., and W. A. Bennett. 2000. Quantification of the role of acclimation temperature in temperature tolerance of fishes. Environmental Biology of Fishes 58:277-288.
- Brett, J. R. 1956. Some principles in the thermal requirements of fishes. The Quarterly Review of Biology 31:75-88.
- Carveth, C. J. 2004. Upper lethal tolerance of spikedace, *Meda fulgida*, exposed to chronic, static and fluctuating temperature treatments. MS thesis. University of Arizona, Tucson.
- Castleberry, D.T., and J. J. Cech. 1986. Physiological-responses of a native and an introduced desert fish to environmental stressors. Ecology 67:912-918.
- Chatterjee, N., A. K. Pal, S. M. Manush, T. Das, and S. C. Mukherjee. 2004. Thermal tolerance and oxygen consumption of *Labeo rohita* and *Cyprinus carpio* early fingerlings acclimated to three different temperatures. Journal of Thermal Biology 29: 265-270.
- Chung, K. S. 2001. Critical thermal maxima and acclimation rate of the tropical guppy, *Poecilla reticulata*. Hydrobiologia 462:253-257.
- Claussen, D. L. 1977. Thermal acclimation in ambystomatid salamanders. Comparative Biochemistry and Physiology 58:333-340.
- Cowles, R. B., and C. M. Bogert. 1944. A preliminary study of the thermal requirements of desert reptiles. Bulletin of the American Museum of Natural History 83:265-296
- Currie, R. J., W. A. Bennett, and T. L. Beitinger. 1998. Critical thermal minima and maxima of three freshwater game-fish species acclimated to constant temperatures. Environmental Biology of Fishes 51:187-200.
- Deacon, J. E., and W. L. Minckley. 1974. Desert fishes. In, G.W. Brown Jr. Editor. Desert biology vol. 2. Academic Press, New York, New York.
- Deacon, J. E., P. B. Schumann, and E. L. Stuenkel. 1987. Thermal tolerances and preferences of fishes of the Virgin River (Utah, Arizona, Nevada). Great Basin Naturalist 47:538-546.

- Diaz, F., and F. Buckle. 1999. Effects of the critical thermal maximum on the preferred temperatures of *Ictalurus puctatus* exposed to constant and fluctuating temperature. Journal of Thermal Biology 24:155-160.
- Dickerson, B.R., and G.L. Vinyard. 1999. Effects of high chronic temperatures and diel temperature cycles on the survival and growth of Lahontan cutthroat trout. Transactions of the American Fisheries Society 128:516-521.
- Douglas, M. E., P. C. Marsh, and W. L. Minckley. 1994. Indigenous fishes of western North America and the hypothesis of competitive displacement: *Meda fulgida* (Cyprinidae) as a Case Study. Copeia 1:9-19.
- Fry, E.J. 1967. Responses to vertebrate poikilotherms to temperature. In, A.H. Rose Editor. Thermobiology. Academic Press, New York, New York.
- Hutchison, V. H., and J. D. Manness. 1979. The role of behaviour in temperature acclimation and tolerance in ectotherms. American Zoology 19:367-384.
- John, K. R. 1964. Survival of fish in intermittent streams of the Chiricahua Mountains, Arizona. Ecology 45:112-119.
- JMP: 4.0.4 (Academic). Copyright 1989-2001. SAS Institute Inc. Distributed by Duxbury Press.
- King, T. L., E. G. Zimmerman, and T. L. Beitinger. 1985. Concordant variation in thermal tolerance and allozymes of tailwater populations of the red shiner, *Notropis lutrensis*. Environmental Biology of Fishes 13:49-57.
- Lass, S., and P. Spaak. 2003. Temperature effects on chemical signaling in predator prey systems. Freshwater Biology 48: 669-677.
- Lowe C. H., and W. G. Heath. 1969. Behavioural and physiological responses to temperature in the Desert pupfish, *Cyprinodon macularius*. Physiological Zoology 42:53-59.
- Lowe, C. H., D. H. Hines, and E. A. Halpern. 1967. Experimental catastrophic selection and tolerance to low oxygen concentration in native Arizona fishes. Ecology 48:1013-1017.
- Lutterschmidt, W. I., and V. H. Hutchison. 1997. The critical thermal maximum: data to support the onset of spasms as the definitive end point. Canadian Journal of Zoology 75:1553-1560.
- Lutterschmidt, W. I., and V. H. Hutchison. 1997. The critical thermal maximum: history and critique. Canadian Journal of Zoology 75:1561-1574.
- MacNutt, M. J., S. G. Hinch, A. P. Farrell, and S. Topp. 2004. The effect of temperature and acclimation period on repeat swimming performance of cutthroat trout. Journal of Fish Biology 65:342-353.
- Matthews, W. J. and L. G. Hill. 1977. Tolerance of the red shiner, *Notropis lutrensis* (Cyprinidae) to environmental parameters. Southwestern Naturalist 22:89-99
- Matthews, W. J., E. Surat, and L. G. Hill. 1982. Heat death of the Orangethroat darter *Etheostoma spectabile* (Percidae) in a natural environment. The Southwestern Naturalist 27:216-217.
- Meffe, G. K., and W. L. Minckley. 1987. Persistence and stability of fish and invertebrate assemblages in a repeatedly disturbed Sonoran Desert stream. The American Midland Naturalist 117:177-191.

- Meffe, G. K., S. C. Weeks, M. Mulvey, and K. L. Kandl. 1995. Genetic differences in thermal tolerance of eastern mosquito fish (*Gambusia holbrooki*, Poecillidae) from ambient and thermal ponds. Canadian Journal of Fisheries and Aquatic Science 52:2704-2711.
- Miller, R. R. 1961. Man and the changing fish fauna of the Southwest. Papers of the Academy of Science, Arts and Letters. Vol. XVI.
- Minckley, W. L., and W. E. Barber. 1971. Some aspects of the biology of the Longfin Dace, a cyprinid fish characteristic of streams in the Sonoran Desert. The Southwestern Naturalist 15:459-464.
- Morgan I. J., D. G. McDonald, and C. M. Wood. 2001. The cost of living for freshwater fish in a warmer, more polluted world. Global Change Biology 7:345-355.
- Moyle, P. B., H. W. Li, and B. A. Barton. 1986. The Frankenstein effect: Impact of introduced fishes on native fishes in North America. pp 415-426. *In*: R.H. Stroud (ed.) Fish culture in fisheries management at Lake Ozark, Missouri, March 31-April 3, 1985. American Fisheries Society, Bethesda.
- Mundahl, N. D. 1990. Heat death of fish in shrinking stream pools. American Midland Naturalist 123:40-46.
- Myrick, C. A., and J. J. Cech. JR. 2000. Swimming performance of four California stream fishes: temperature effects. Environmental Biology of Fishes 58:289-295.
- Otto. R.G. 1973. Temperature tolerance of mosquito fish, *Gambusia affinis* (Baird and Girard). Journal of Fish Biology 5:575-585
- Poole, G. C., and C. H. Berman. 2001. An ecological perspective on in-stream temperature: natural heat dynamics and mechanisms of human caused degradation. Environmental Management 27:787-802.
- Rinne, J. N., J. E. Johnson, B. L. Jensen, A. W. Ruger, and R. Sorenson. 1986. The role of hatcheries in the management and recovery of threatened and endangered fishes. pp 271-286. *In*: R.H. Stroud (ed.) Fish culture in fisheries management at Lake Ozark, Missouri, March 31-April 3, 1985. American Fisheries Society, Bethesda.
- Rinne, J.N. 1989. Physical habitat use by loach minnow, *Tiaroga cobitis* (Pisces: Cyprinidae) in southwestern desert streams. The Southwestern Naturalist 34:109-117.
- Rutledge, C. J., and T. L. Beitinger. 1989. The effects of dissolved-oxygen and aquatic surface respiration on the critical thermal maxima of 3 intermittent stream fishes. Environmental Biology of Fishes 24:137-143
- Selong, J.H., T. E. McMahon, A. V. Zale, and F. T. Barrows. 2001. Effect of temperature on growth and survival of bull trout, with application of an improved method for determining thermal tolerance in fishes. Transactions of the American Fisheries Society 130:1026-1037.
- Smale, M. A., and C. F. Rabeni. 1995. Hypoxia and hypothermia tolerances of headwater stream fishes. Transactions of the American Fisheries Society 124:698-710.
- Stauffer, J. R., E. L. Melisky, and C. H. Horcutt. 1984. Interrelationship among preferred, avoided, and lethal temperatures of 3 fish species. Archiv Fur Hydrobiologie 100:159-169.
- U.S. Fish and Wildlife Service. 1991. Spikedace, *Meda fulgida*, recovery plan. U.S. Fish and Wildlife Service, Albuquerque, New Mexico.

- U.S. Fish and Wildlife Service.1991. Loach minnow, *Tiaroga cobitis*, recovery plan. U.S. Fish and Wildlife Service, Albuquerque, New Mexico.
- Widmer, A. M. 2004. Temperature tolerance of loach minnow under acute, chronic and fluctuating thermal regimes. MS thesis. University of Arizona, Tucson.
- Zimmerman, U. D., and C. L. Kucera. 1977. Catastrophic mortality of stream fishes trapped in shrinking pools. The American Midland Naturalist 97:469-478.

Table 1. Fish species, sorted by family, used in critical thermal maximum tests, with total length (mm) and status in Arizona.

Family and Scientific Name	Common Name	Total Length (mm)	Status in Arizona
Cyprinodontidae			
Cyprinodon macularius	Desert Pupfish	27 - 42	Native
Cyprinidae			
Rhinichthys osculus	Speckled Dace	37- 68	Native
Tiaroga cobitis	Loach minnow	34 - 49	Native
Agosia chrysogaster	Longfin Dace	29 - 44	Native
Meda fulgida	Spikedace	34 - 51	Native
Cyprinella lutrensis	Red Shiner	38 - 60	Nonnative
Pimephales promelas	Fathead Minnow	72 - 80	Nonnative
Gila intermedia	Gila Chub	49 - 64	Native
Gila robusta	Roundtail Chub	34 - 51	Native
Gila elegans	Bonytail Chub	24 - 43	Native
Catostomidae			
Catostomus clarki	Desert Sucker	36 - 60	Native
Xyrauchen texanus	Razorback Sucker	44 - 64	Native
Centrachidae			
Lepomis macrochirus	Bluegill Sunfish	92 - 113	Nonnative
Lepomis cyanellus	Green Sunfish	48 - 109	Nonnative
Micropterus salmoides	Largemouth Bass	51 - 79	Nonnative
Peociliidae			
Poeciliopsis occidentalis	Gila Topminnow	25 - 50	Native
Gambusia affinis	Mosquito Fish	26 - 46	Nonnative
Ictaluridae			
Ameiurus natalis	Yellow Bullhead	49 - 116	Nonnative

Table 2. Upper lethal tolerance of selected species found throughout Arizona. Where available, CTM results are presented with loss of equilibrium as the endpoint. Thermal tolerance is presented with a 95% confidence interval unless otherwise noted.

Species	Method	Rate of Change (°C)	Acclimation temperature (°C)	Upper lethal (°C)	Reference
Pimephales promelas	CTM	0.3	32	40.4 (SD=0.25)	Richards and Beitinger, 1995
Ictalurus punctatus	CTM	0.3	25	38.7 (SD=0.36)	Currie et al. 1998
			30	40.3 (SD=0.29)	
Catostomus latipinnis	CTM	0.24	25	37.0 (SD=0.29)	
Plagopterus argentissimus	CTM	0.24	25	39.5 (SD=0.21)	Deacon et al. 1987
Lepidomeda mollispinis mollispinis	CTM	0.24	25	37.0 (SD=0.44)	
Lepomis cyanellus	CTM	0.017	26	32.7 (SD = 0.75)	Smale and Rabeni, 1995
Lepomis macrochirus	CTM	1.0	25	36.3- 37.0	Holland et al. 1974
			30	37.4-39.6	
Micropterus salmoides	CTM	0.3	25	36.7 (SD = 0.59)	Currie et al. 1998
			30	38.5 (SD = 0.34)	
Cyprinella lutrensis	СТМ	0.3	25	36.5 – 38.0 <u>+</u> 0.41-0.94	King et al. 1985
			30	39.6 (SD = 0.23)	Rutledge and Beitinger, 1989
Rhynicthys osculus	CTM	0.3	20	32.4 <u>+</u> 1.90	Castleberry and Cech, 1992
	CTM	0.24	25	36.8 (SD=0.63)	Deacon et al. 1987
Gambuisa affinis	CTM	0.3	25	39.5	Otto 1973
			30	42.3	
Cyprinodon macularius	CTM	0.5	30	42 (SD 0.30)	Lowe and Heath, 1969

Table 3. Loss of equilibrium temperatures for native and nonnative species found throughout Arizona. Loss of equilibrium was recorded for two acclimation temperatures including 25° C and 30° C. Confidence intervals (95%) are indicated for each value. Species are ranked by CTMax value for an acclimation temperature of 25° C.

Species	CTMax at 25°C	CTMax at 30°C	Upper Lethal Tolerance at 25°C	Upper Lethal Tolerance at 30°C
Desert Pupfish	40.0 <u>+</u> 0.26 °C	41.3 <u>+</u> 0.32 °C	41.8 <u>+</u> 0.23 °C	42.7 <u>+</u> 0.28 °C
Mosquitofish	39.5 <u>+</u> 0.32 °C	41.4 <u>+</u> 0.76 °C	40.7 <u>+</u> 0.22 °C	42.1 <u>+</u> 0.44 °C
Gila Topminnow	38.4 <u>+</u> 0.35 °C	41.1 ± 0.35 °C	39.4 <u>+</u> 0.33 °C	42.1 <u>+</u> 0.28 °C
Longfin Dace	38.2 <u>+</u> 0.08 °C	40.5 <u>+</u> 0.16 °C	38.9 <u>+</u> 0.14 °C	41.1 <u>+</u> 0.13 °C
Yellow Bullhead	38.0 <u>+</u> 0.44 °C		39.8 <u>+</u> 0.92 °C	
Largemouth Bass	37.8 <u>+</u> 0.28 °C		39.1 <u>+</u> 0.40 °C	
Red Shiner	37.6 <u>+</u> 0.62 °C	39.7 <u>+</u> 0.27 °C	39.5 <u>+</u> 0.32 °C	40.9 <u>+</u> 0.23 °C
Green Sunfish	37.4 <u>+</u> 0.53 °C	40.2 <u>+</u> 0.50 °C	39.3 <u>+</u> 0.20°C	41.5 <u>+</u> 0.21 °C
Bonytail Chub	37.2 <u>+</u> 0.42 °C	39.0 <u>+</u> 0.26 °C	38.7 <u>+</u> 0.36 °C	40.2 <u>+</u> 0.21 °C
Gila Chub	37.0 <u>+</u> 0.20 °C	38.1 <u>+</u> 0.30 °C	38.3 <u>+</u> 0.24 °C	39.0 <u>+</u> 0.29 °C
Razorback Sucker	36.7 <u>+</u> 0.23 °C	39.1 <u>+</u> 0.33 °C	39.1 <u>+</u> 0.17 °C	40.3 <u>+</u> 0.12 °C
Roundtail Chub	36.6 <u>+</u> 0.11 °C		38.0 <u>+</u> 0.30 °C	
Fathead Minnow	36.1 <u>+</u> 1.17 °C		36.9 <u>+</u> 1.07 °C	
Bluegill Sunfish	35.8 <u>+</u> 0.38 °C	38.7 <u>+</u> 0.27 °C	37.3 <u>+</u> 0.32 °C	39.6 <u>+</u> 0.19 °C
Loach Minnow	35.3 <u>+</u> 0.20 °C	36.1 <u>+</u> 0.32 °C	36.5 <u>+</u> 0.14 °C	36.8 <u>+</u> 0.47 °C
Desert Sucker	35.1 <u>+</u> 0.30 °C	36.7 <u>+</u> 0.28 °C	36.9 <u>+</u> 0.16°C	37.6 <u>+</u> 0.17 °C
Spikedace	34.7 <u>+</u> 0.48 °C	36.9 <u>+</u> 0.68 °C	37.0 <u>+</u> 0.35 °C	39.1 <u>+</u> 0.35 °C
Speckled Dace	34.4 <u>+</u> 0.42 °C	35.8 ± 0.57 °C	36.0 <u>+</u> 0.44 °C	36.9 ± 0.28 °C

Table 4. Acclimation response ratio for all species acclimated at 25 and 30°C ($\Delta T = 5$ °C). Acclimation response ratio determined for both CTMax ($\Delta CTM/\Delta T$) and upper lethal tolerance ($\Delta ULT/\Delta T$) values.

Species	ΔCTM	ΔCTM/ ΔΤ	ΔULT	ΔULT/ΔΤ
Bluegill Sunfish	2.9°C	0.58	2.3°C	0.46
Green Sunfish	2.8°C	0.56	2.2°C	0.44
Gila topminnow	2.7°C	0.54	2.7°C	0.54
Razorback Sucker	2.4°C	0.48	1.2°C	0.24
Longfin dace	2.3°C	0.46	2.2°C	0.44
Spikedace	2.2°C	0.44	2.1°C	0.42
Red Shiner	2.1°C	0.42	1.4°C	0.28
Mosquito fish	1.9°C	0.38	1.4°C	0.28
Bonytail Chub	1.8°C	0.36	1.5°C	0.30
Desert Sucker	1.6°C	0.32	0.7°C	0.14
Speckled Dace	1.4°C	0.28	0.9°C	0.18
Desert Pupfish	1.3°C	0.26	0.9°C	0.18
Gila Chub	1.1°C	0.22	0.7°C	0.14
Loach minnow	0.8°C	0.16	0.3°C	0.06